

# Redescription of the genus *Modiomytilus* Griffin, 1990 (Bivalvia: Mytilidae) from Southern Patagonia with remarks on the paleobiogeography of the genus

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## ABSTRACT

*Modiomytilus* Griffin, 1990, was based on composite molds collected from Cenozoic rocks in southern Patagonia. The type species comes from the early Miocene Centinela Formation, exposed along the southern shore of Lake Argentino. An additional species is known from the Eocene Río Turbio Formation, which outcrops only at the southwestern corner of Santa Cruz Province. New material preserved as original shell was collected recently in beds referred to the Centinela Formation exposed in the same area as the Río Turbio Formation, about 150 km south of Lake Argentino. Enough detail is preserved in collected the shells to warrant an emended diagnosis and a new and more complete description of the genus, as they provide a set of characters not recorded in the currently known material of any of the species described. The shells clearly belong to the type species, i.e., *Modiomytilus argentinensis* Griffin, 1990. These characters, among which are included the ligament, adductor muscle scar, pallial line, and byssal retractor muscle scar allow a reinterpretation of this genus and confirm its validity. At the same time these new morphological characters may be potentially useful for further phylogenetic analyses and a new interpretation of the currently available material, a prerequisite for understanding the palaeobiogeographic history of this genus.

*Additional keywords:* Early Miocene, middle Eocene, shell morphology

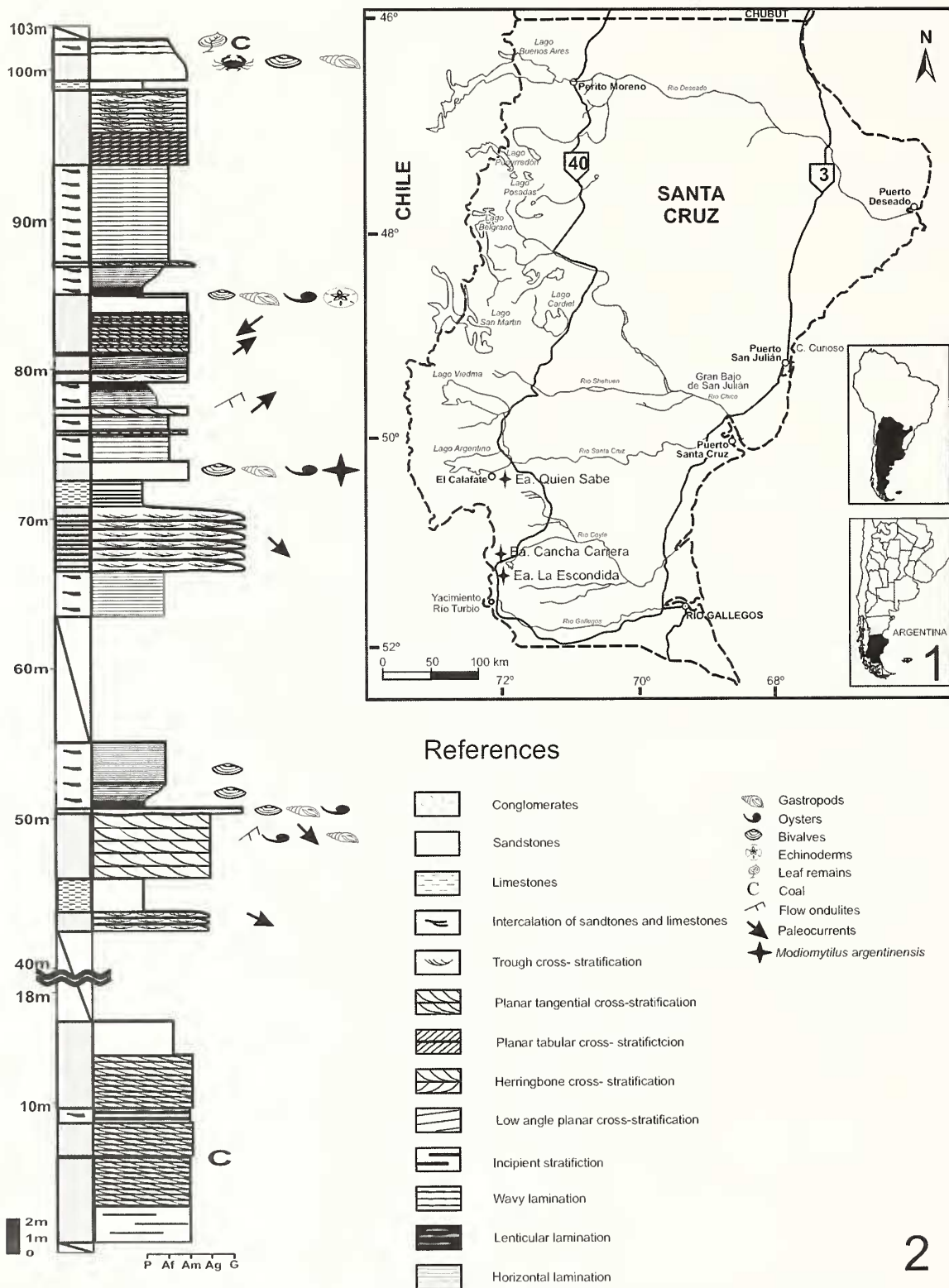
## INTRODUCTION

The genus *Modiomytilus* was introduced to include two species, *Modiomytilus argentinensis* Griffin (1990: 377–380), from the early Miocene Centinela Formation, and *Modiomytilus mercecrati* Griffin (1990: 380–381, fig. 1, 2) from the Eocene Río Turbio Formation, in Santa Cruz

Province. The genus description was based on composite molds in which no part of the shell was preserved. Also belonging in this genus are *Mytilus* aff. *chorus lauthali* Molina sensu Ihering (1907: 273–274), from the “Patagonian” beds in the Ñirihuan basin (northern Patagonia) and *Mytilus pseudochorus* Doello-Jurado (1922: 86–90, fig. 1) from the “Patagonian” beds of Sierra de los Baguales (Santa Cruz), and additional non-figured specimens from San Julián. *Mytilosootus arcuatus* Stilwell and Zinsmeister, (1992: 54–56, pl. 3 fig. a), from the Eocene La Meseta Formation in Seymour Island, Antarctica, was based on an internal mold belonging in *Modiomytilus* too.

The aim of this contribution is to re-describe this genus more accurately based on new specimens recently collected in the Centinela Formation in southwestern Santa Cruz. This material confirms some of the original diagnostic characters and reveals the presence of other particular features that better distinguish this taxon from other Mytilidae. Among these are shell thickness, the presence of a well developed and buttressed anterior adductor muscle scar coalescent with a large byssal retractor scar, and a pitted resilial ridge, together with a thickened hinge plate with growth lines only. Biogeographic and stratigraphic distributions of the species involved suggest that the genus had an austral origin and a lifespan ranging from the at least the late Eocene through the early Miocene. Its ecological requirements probably played an important role, as it is not common. However, in the beds where it does occur—deposited in shallow, possibly restricted marine environments—it is usually abundant, and sometimes the only mollusk taxon present.

The specimens studied are deposited at the División de Paleozoología de Invertebrados Collection, Museo de La Plata, Buenos Aires, Argentina (MLP). The term ichnospecies is abbreviated “isp.”



References

- Conglomerates
- Sandstones
- Limestones
- Intercalation of sandstones and limestones
- Trough cross-stratification
- Planar tangential cross-stratification
- Planar tabular cross-stratification
- Herringbone cross-stratification
- Low angle planar cross-stratification
- Incipient stratification
- Wavy lamination
- Lenticular lamination
- Horizontal lamination
- Gastropods
- Oysters
- Bivalves
- Echinoderms
- Leaf remains
- Coal
- Flow ondulites
- Paleocurrents
- Modiomylitus argentinensis*

Figure 1-2. Location map and stratigraphic section. 1. Location map of the fossil locality in Santa Cruz Province, Argentina. 2. Studied stratigraphic section showing bed with mytilids.

## GEOLOGICAL SETTING (Figure 2)

Rocks deposited during the Cenozoic Patagonian transgression are included in several units of slightly variable lithology and exposed over a wide area of Patagonia. Located in the southwestern corner of Santa Cruz Province, these rocks are known as Centinela Formation (Furque and Camacho, 1972). This unit is discontinuously exposed along the foothills of the Andes for a distance of about 500 km, approximately between Lake Pueyrredón (47°48' S, 70°47' W) and Estancia La Escondida (51°24' S, 72°10' W). The new specimens collected come from this southernmost locality, where the Centinela Formation overlies the continental plant and coal-bearing Oligocene Río Leona Formation (Figure 1).

Marensi et al. (2005) reported that the Río Leona Formation comprises a fining-upward succession of facies deposited in high-energy fluvial environments at the base, giving way to low energy meandering and anastomosed rivers at the top. Such a variation in the fluvial style of this unit is probably linked to the paleogeographic evolution of the southwestern corner of the Austral Basin. The base probably represents a high gradient piedmont context, while the top of the unit reveals the presence of a low coastal plain at the time the unit was deposited. Approximately 25 to 22 million years ago this coastal plain was covered by the Patagonian transgression. Accordingly, the Río Leona and Centinela formations constitute a depositional sequence of Oligocene to early Miocene age (Marensi et al., 2002).

At the fossil locality studied, the Centinela Formation comprises fine to medium sandstones, sometimes with fossil mollusks, with subordinate conglomeratic sandstones, fine conglomerates, coquinas and mudstones deposited in a shallow littoral marine environment (Malumián et al., 2000). Contact with the overlying Santa Cruz Formation is masked by Recent deposits. However, the restricted outcrops of the Centinela Formation in the area and the fact that the Santa Cruz Formation in some places directly overlies the Río Leona Formation suggest that there may be an unconformity separating the two units (Malumián et al., 2000).

The studied locality lies within land belonging to Estancia La Escondida, about 20 km to the north of the mining town of Río Turbio. Contrary to localities in the Lake Argentino area, at Estancia La Escondida the Centinela Formation is thinner and geographically restricted, i.e., it is exposed only along a narrow 12 km N–S stretch between Estancia Las Tres Marías (51°30'00" S, 72°16'67" W) and Estancia La Primavera (51°27'00" S, 72°13'60" W) (Malumián et al., 2000).

The section is 103 m thick and contact with the underlying Río Leona Formation is transitional, as at other localities in southwestern Santa Cruz such as Estancia 25 de Mayo and Estancia La Siberia (Casadio et al.,

2000; Rodríguez Raising et al., 2006). Because of the loose and poorly resistant nature of the pelitic facies at the top of the Río Leona and bottom of the Centinela formations, the contact itself is not exposed.

The lowermost exposed beds of the Centinela Formation are about 16 m of medium cross-stratified sandstones with pelitic layers bounding the fore-sets. At the base of some of the sets there are thin layers of conglomerates and coarse sandstones. These beds carry *Ophiomorpha* isp. Intercalated among them are medium to fine sandstones and heterolithic beds.

The overlying 26 m are covered, probably because they include loose heterolithic facies that are easily meteorized, as observed at other localities where the unit is exposed such as Estancia La Siberia (Rodríguez-Raising et al., 2006). The section continues upward with 24 m of mudstone and heterolithic beds with medium- to coarse-grained sandstone and subordinate conglomerates. The coarser facies carry a rich invertebrate fauna and burrows referred to *Thalassinoides* isp. and *Ophiomorpha* isp.

Overlying these beds are 4.5 m of coarse sandstone and conglomerates with trough cross-stratification, followed by 1.5 m of siltstone and 1.25 m of fine to medium muddy sandstone with abundant remains of bivalves—including the studied mytilids. At the base of the sandstone there are bivalve burrows excavated into the underlying mudstone. This bed carries *Valdesia dalli* (Ihering, 1897); *Perissodonta ameghinoi* (Ihering, 1897); *Polinices santacruzensis* Ihering, 1907; *Modiomylilus argentinensis* Griffin, 1990 (disarticulated and bioeroded); *Gregariella* sp.; *Modiolus arctus* (Feruglio, 1935); "*Ostrea*" *hatcheri* Ihering, 1902 (right valve); *Cardium* sp. (disarticulated); Tellinidae indet.; *Retrotapes striatolamellata* (Ihering, 1907); *Panopea bagualesia* Ihering, 1899 (in life position); *Panopea nucleus* (Ihering, 1899); *Laternula* sp. Some of the valves are lying convex down with abundant bioerosion on their inner surface. Specimens of *Panopea* in life position are common and one articulated *Laternula* was observed.

The next 28 m are heterolithic beds with medium sandstones with cross-stratification and constituting cosets up to 5 m thick. Two sandstone beds carry bivalve shells, some of them (*Panopea* sp.) in life position, echinoderms, gastropods, and—within the bed closest to the top of the section—crab remains. The top of the section includes heterolithic beds with leaves and plant debris.

The presence of *Panopea* in life position suggests that the bed carrying most of the fossils was deposited in a subtidal environment. Bioerosion and encrusting of the shell inner surface suggest that they laid exposed on the sea floor during a period of low sea level long enough to allow colonization. The abundance of shells with different degrees of weathering also suggests a period with low sedimentation. According to these observations, the mytilid-bearing bed was deposited during a low sedimentation period in a subtidal normal marine environment. This could be linked to a maximum flooding surface of the Patagonian transgression in the area.



## SYSTEMATIC PALEONTOLOGY

Superfamily Mytiloidea Rafinesque, 1815

Family Mytilidae Rafinesque, 1815

Subfamily Modiolinae Keen, 1958

Genus *Modiomytilus* Griffin, 1990

**Type Species:** *Modiomytilus argentinensis* Griffin, 1990; original designation.

**Description:** Shell modioliform, umbones not terminal; well defined ridge running in a wide curve from umbones to posterior ventral end; ligament about one half of total length of shell; anterior part contained within narrow, deep ligament groove running along dorsal margin of thickened hinge plate; resilial ridge not preserved, but regular pits along posterior part of nymphs suggest that it was pitted (Figure 4); pits wider dorsally, ventrally narrowing, and curving forward to join preceding ones into anterior groove; obsolete posterior lateral tooth on right valve and shallow groove on anterior hinge plate; anterior adductor muscle scar (AAMS) large, placed on low buttress, with anterior part encroached by vertical wall of thick anterior part of shell (Figure 3); vertical wall with well marked rounded pits and with short strong irregular ribs near intersection with AAMS, running perpendicular surface of latter; surface of AAMS with strong parallel ridges, reflecting on prismatic layer the underlying ribs on inner shell surface in this region; anterior retractor muscle scar large and rounded, placed at dorsal posterior end of buttress supporting AAMS (Figure 5); pallial line strongly incised, irregularly pitted, meeting AAMS (Figure 6); nacreous inner surface; ornamentation of commarginal undulations (Figure 7).

**Species Included:** The type species *Modiomytilus argentinensis* Griffin, 1990 comes from the early Miocene Centinela Formation exposed along the southern margin of Lake Argentino, in southwestern Santa Cruz. The additional material described herein was collected from rocks referable to this unit as exposed at Estancia La Escondida approximately 40 kilometers north of Río Turbio. The oldest species recorded are the Eocene *Modiomytilus arcuatus* (Stilwell and Zinsmeister, 1992) from the La Meseta Formation in Antarctica (Stilwell and Zinsmeister, 1992, p. 54–56, pl. 3 fig. a), and *Modiomytilus mercerati* Griffin (1990: 380–381, figs 3–4), from the Río Turbio Formation in southwestern Santa Cruz. *Modiomytilus pseudochorus* (Doello-Jurado, 1922, p. 3–6, fig. 1) is known only by the type specimens, which come from the early Miocene Monte León Formation exposed at the mouth of the Santa Cruz River. No additional material has ever been reported of this species. *Modiomytilus haultali* (Ihering, 1907) occurs in Cenozoic beds exposed in northwestern Patagonia (Ihering, 1907), probably equivalent to the Monte León and Centinela formations.

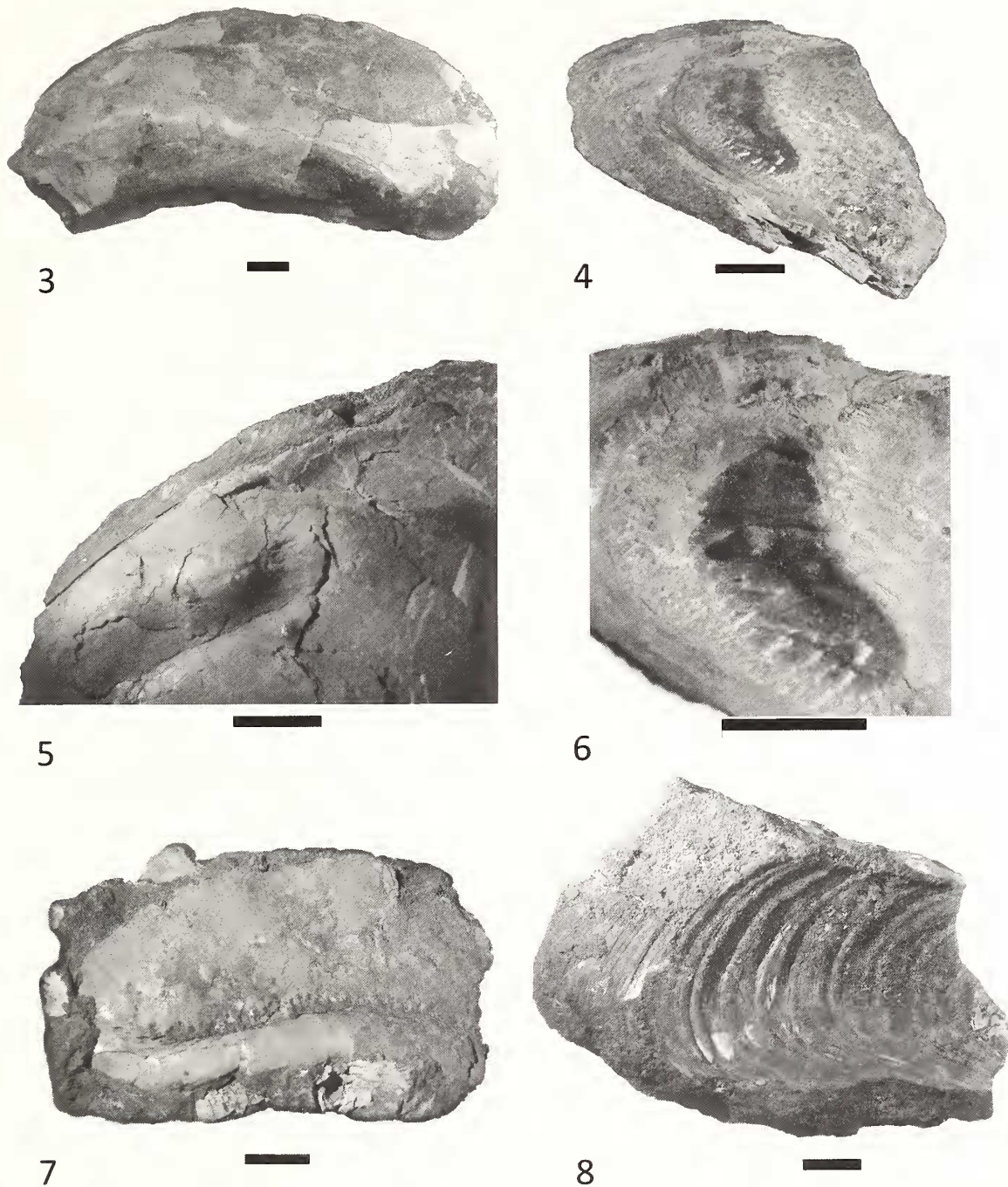
**Remarks:** Species of *Modiomytilus* could not be included in any of the currently accepted supraspecific taxa of Cenozoic Mytilidae. *Mytilus* Linnaeus (1758: 104) has a proportionally much more reduced anterior adductor muscle scar and thinner shells; the external ornamentation is smooth, while in *Modiomytilus* the shell surface shows commarginal undulations. *Aulacomya* Mörchl (1853: 53) differs considerably by its radial ribs, its lack of an anterior adductor muscle, and its unpitted resilial ridge. *Perna* Retzius (1788: 20) shows—as does *Modiomytilus*—a pitted resilial ridge and a nacreous inner surface, but it is missing an anterior adductor muscle scar. The Recent *Mytella* Soot-Ryen (1955: 47) shares the pitted resilial ridge but the commarginal ornamentation of this genus is much weaker and regular. The southern Pacific *Notobotula* Fleming, (1959: 170), has a quite large muscle scar very much like that of *Modiomytilus* but shows no evidence of the strong parallel ridges, and it lacks commarginal ornamentation except for growth lines. The Recent *Semimytilus* Soot-Ryen (1955: 25), from the west coast of South America, differs by its compact resilial ridge and smooth surface. The Oligocene–Recent *Crenomytilus* Soot-Ryen (1955: 23), shows a distinct thickened anterior adductor scar like in *Modiomytilus*, but without the complexity of the scar surface of the latter; it also presents terminal umbones, a compact resilial ridge, and an obliquely striated shell that is clearly different from *Crenomytilus*. *Choromytilus* Soot-Ryen (1952: 121) is easily distinguishable because of its compact resilial ridge, the absence of an anterior adductor muscle, its typical hinge tooth, and its smooth surface.

***Modiomytilus argentinensis* Griffin, 1990**

(Figures 2–7)

*Modiomytilus argentinensis* n. sp.; Griffin, 1990: 379–380, figs. 1, 2

**Description:** Shells large (maximum estimated length = 154.5 mm), mytiliform, with subterminal anterior umbones. Dorsal margin convex and smoothly merging into narrowly curved posterior margin. Ventral margin concave, maximum concavity just in front of shell midlength. Shell thickness very variable depending on area of shell. Shell very thick at umbonal end, reaching 14.47 mm at the posterior end of the AAMS). Shell thinning out in a posterodorsal direction, measuring only a few millimeters at posterodorsal end. Anterior margin strongly thickened just below umbones; margin forming a narrow marginal plate densely packed with growth lines, reflecting the shell thickness at this sector of the valves. Hinge without traces of dentition. Ligament running along approximately 0.6 mm of dorsal margin, which is slightly thickened to hold resilial ridge. Anterior part of preserved ligament groove narrow and curved along anterior dorsal margin. Ligament groove occupying a wider strip along margin towards posterior end, ending abruptly and bounded by a faint ridge weakening even further towards the dorsal margin, which it does not



**Figures 3–8.** *Modiomutilus argentinensis*. **3.** Specimen with conjoined valves (anterior end missing), showing remains of inner layer of shell, MLP-23197. **4.** Right valve internal view showing a general view of the anterior adductor muscle scar (AAMS) and well developed hinge plate, MLP-23190. **5.** Detail of ligament showing marks of pitted resiliar ridge along dorsal margin. Specimen decorticated, MLP-23197. **6.** Detail of the AAMS. Note subspherical protuberance on AAMS surface. Also anterior vertical surface and strong ridges beneath AAMS surface, MLP-23190. **7.** Left valve internal view showing irregularly pitted pallial line, MLP-23182. **8.** External mold of right valve showing commarginal folds (posterior half of shell), MLP-23205. Scale bars = 1 cm.

reach in any of the available specimens. Ligament groove showing clearly pitted nature of resiliar ridge at mid-length, evident in specimens with shell material partly adhered to internal molds, but not so in specimens in

which shell is missing, including the type specimens. Area between resiliar ridge and dorsal margin of shell flat, but crossed by very shallow curved depressions that begin at resiliar ridge and widen towards margin



(Figure 5). Internal surface of shell generally smooth and not reflecting external ornamentation, but showing anterior adductor muscle scars, anterior byssal retractor scars, pallial line and granulations. AAMS placed near anterior end, large (20.7 mm × 13.3 mm), buttressed and kidney-shaped, i.e., scar evenly rounded anteriorly and showing a fairly deep concavity at mid-length posteriorly; anterodorsal half of AAMS more inflated, posterior half slightly more elongated; AAMS bounded anteriorly by steeply inclined inner surface of shell (forming an angle of about 100°), acquiring again an approximately horizontal position near margin, thus rendering a reflected appearance to anterior inner shell surface. Surface of AAMS not smooth, but covered by straight anteroposteriorly directed rods, subquadrangular in section and more densely packed and thicker against anterior boundary of scar, tapering towards posterior edge of AAMS. Vertical surface of shell immediately adjacent to anterior outline of AAMS densely reticulated. AAMS surface with a hemispherical knob-like structure at mid-width and at base of anterior half of scar. Muscle pad rapidly sloping down to general shell surface behind posterior edge of AAMS, but not as steeply as rising shell surface anterior to scar. Anterior byssal retractor muscle scar large, rounded, placed just above AAMS pad as it meets anterodorsal margin of shell. Pallial line entire, strongly marked, and pitted throughout its preserved length, especially along ventral concave margin of shell. Posterior adductor muscle scars unavailable for observation, because posterior region of shell was not preserved in examined specimens. Outer surface of shell strongly ornamented with commarginal undulations. Intercostal spaces crossed by fine and barely noticeable radial striations.

**Geological Occurrence:** All specimens come from the upper section of the Centinela Formation exposed at Estancia La Escondida, located about 20 km North of the mining town of Río Turbio, Santa Cruz Province (51°24'21.76" S, 72°10'2.35" W).

**Material Examined:** MLP-23180: three RV internal molds partly covered by shell matter; MLP-23182: two left valve fragments with shell, showing pitted pallial line; MLP-23186: two fragments of anterior end RV, shell preserved, showing a pitted resilial ridge and anterior adductor muscle scar; MLP-23190: three anterior end fragments of RV, internal view, shell preserved, showing anterior adductor muscle scar; MLP-23195: a fragment of internal mold of LV, shell preserved on margins. MLP-23197: one specimen with valves conjoined without the anterior end, showing remains of inner layer of shell; MLP-23199: LV internal mold fragment with preserved shell on ventral margin; MLP-23205: fragment of external mold of RV, showing commarginal folds; MLP-23212: fragment of anterior RV.

**Remarks:** The description provided above differs substantially from the original description of this species and consequently from the original generic description, as all

previously known specimens consisted of only internal and composite molds in which many characters now available were not observed. Thus, a new interpretation of this taxon strengthens the taxonomic placement suggested for other species in which the shell still remains unknown. The muscle scar appears as a strong pad, more or less oval in outline. Width of pad is about 50% of length. However, the new specimens described herein show a number of distinct peculiarities of this muscle scar that cannot be observed in any of the molds previously available. Among these are the numerous vertical striations on the shell surface that bound the muscle scar anteriorly. These striations are a conspicuous feature of the shells, but are not preserved on the molds.

Comparison of this species with the other species referred to this genus must necessarily be tentative, until specimens of the latter are found with preserved shells. However, the original comparisons of *Modiomytilus argentinensis* with *Modiomytilus mercerati* are confirmed by the new material described herein. The type series of *M. argentinensis* are all composite molds showing no traces of shell. Nevertheless, the size and shape of the anterior adductor muscle scars agree perfectly with those in the new shells from Estancia La Escondida. The shell interior of these appears to be smooth (except for the muscle scars and granulated texture on some areas). On the composite molds, this surface is superimposed onto the outer shell ornamentation, which shows the same wavy and anastomosing pattern as the shells newly described herein.

Similarly, all known specimens of *Modiomytilus mercerati*, Griffin, 1990 are composite molds. While the ornamentation in these specimens is also very similar to that of the type species, the shells appear to be considerably more inflated and the anterior adductor muscle scar is slightly smaller. These differences are confirmed by the new specimens described herein, in spite of the fact that none of them have a complete shell preserved. Yet, the internal molds in the new specimens, while missing the external ornamentation, show similar shell inflation to that of *M. argentinensis*, and are never as inflated as the molds of *M. mercerati*.

All known specimens of *M. pseudochorus* (Doello Jurado, 1922) are internal molds missing any trace of shell. However, these molds also show the large anterior adductor muscle scar and an outline and shape similar to those of the new specimens of the type species described herein. *Modiomytilus lauthali* (Ihering) from northwestern Chubut, exhibit a similar shell shape, although they appear to be slightly more elongate. The outer shell ornamentation is similar to that of the type species. Unfortunately, no interiors are well-enough preserved to show details of the muscle scars.

**Biogeography:** The geographic and stratigraphic ranges of the species included in *Modiomytilus* suggest that it originated in the Southern realm during the Paleogene, being restricted to shallow marine environments of Antarctica and along the Atlantic coast of Patagonia. The

earliest species of *Modiomytilus* appears to have been *Mytilosootus arcuatus* Stilwell and Zinsmeister, from the La Meseta Formation in Seymour Island (Antarctica). While incompletely preserved, the shells fit well in *Modiomytilus*. Very little is known about the Antarctic species as the internal molds have not preserved much of the internal shell features; however, they do show the unique large anterior adductor muscle scars. The La Meseta Formation was deposited during the late early Eocene (Stilwell and Zinsmeister, 1992), slightly earlier than the Río Turbio Formation, the age of which ranges from middle Eocene to early late Eocene (Malumián and Caramés, 1997). Mytilids in general have planktotrophic larvae and therefore show considerable dispersal potential. In addition, their byssate life habits also add to this capability, as they may raft across considerable distances attached—in the southern hemisphere—to kelp or driftwood (Fraser et al., 2010). Postlarval dispersal may be also possible by means of byssal threads (Sigurdsson et al., 1976; Baker, 1997). The Cenozoic fossil record in Antarctica is restricted to the Antarctic Peninsula and McMurdo Sound (GSA, Stilwell and Feldmann, 2000). It appears that Antarctic-South American dispersal likely took place during the early Cenozoic, as the Circum Antarctic Current had not been yet fully established, although surface water may have circulated to some extent in a West-East direction. This would have enabled the dispersal of other members of the Cenozoic faunas which are known to occur in high latitudes during the Paleogene, but appear in younger rocks in South America (Manceñido and Griffin, 1988; Beu et al., 1997; Casadío et al., 2010)

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